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GROWTH AND SIZE OF SHOOT POPULATIONS IN CANOPY LAYERS OF *QUERCUS LEUCOTRICHOPHORA* (FAGACEAE)

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ABSTRACT. A growth analysis was made of first-order lateral shoots in three canopy layers of an evergreen Himalayan oak species (*Quercus leucotrichophora* or banj oak), growing under three banj oak forest stands at altitudes of 1160–1800 m above sea level. Determinate patterns of shoot growth differed by 7–15 days between lower and higher altitudes. Different levels of statistical significance were obtained for shoot length, diameter, and leaf numbers in extension growth during the first and second year of the study. At canopy level, the size of second-year shoots exceeded that of first-year shoots. The lower canopy layer differed significantly in shoot length from those of upper and middle layers, reflecting differences in resource-capturing ability. Leaf number per shoot was significantly higher in high altitude mixed-species forest than in oak-dominated stands. The author suggests that tree growth studies such as this analysis are useful not only in understanding the ecology of the species but also in conservation management.

Key words: *Quercus leucotrichophora,* banj oak, shoot growth, India, Himalaya

INTRODUCTION

Conserving and managing forest ecosystems requires a knowledge of the ecological adaptations and growth characteristics of the trees (Ramakrishnan et al. 1982). Tree growth patterns can be attributed to tree productivity. Shoot productivity of individual trees of the same species depends on ecological adaptability and thus on allocation requirements that are location and site specific.

Tree species comprise populations at two levels: traditional populations of individual trees, each developing from a single seed; and populations of tree parts, such as shoots, leaves, or buds found within each individual (Harper 1980, McGraw 1989). Harper (1968) first proposed the study of individual plants as populations of repeating units, particularly the unit formed by the leaf and associated internode and axillary meristem. Populations of parts, such as the size frequency of shoots, can be ascribed to their productivity level or deployment of the photosynthate (Grime 1979). Leaf development data then can be useful in understanding the ecology of trees and potentially in their management (Montenegro et al. 1997).

Banj oak (*Quercus leucotrichophora* Camus ex Bahadur, Fagaceae) is an evergreen hardwood Himalayan species that often grows independently in pure and/or mixed stands at 1200–2400 m (Polunin & Stainton 1984). A slow growing and moderate light demanding species (Badola et al. 1992), it has a hard wood, apt to warp and split, that villagers use to build houses and make ploughs. Where agroforestry is practiced, banj oak is especially important because of its excellent fodder and fuelwood qualities. In addition, it provides resources such as charcoal, timber, food, medicine, tannin, oil, and cork. The trees have massive root systems, are wind-firm, and coppice well (Ghildyal 1991). Himalayan oaks can minimize biotic pressures to form stable and pure communities; thus they can act both as pioneer and climax species (Singh & Singh 1983).

Expanding human populations, rapid rates of deforestation, and forest fires in Himalaya are placing pressure on oak forests. Various management systems for oak stands are in practice, such as lopping regimes, selection and shelterwood cuttings, and coppicing. Ghildyal (1991) recommended restricted lopping regimes that allow one quarter of the canopy to remain intact at all times. Understanding shoot growth behavior in various canopy layers of these trees may provide clues on selecting which portion of the canopy must remain intact during lopping operations.

One objective of this study is to understand how various environments influence the growth and size frequency distribution of shoots at three canopy layers of banj oak growing in natural forests under different management systems. A second objective is to understand whether shoots behave as relatively independent physiological units (Watson & Casper 1984).

MATERIALS AND METHODS

Three study sites were selected near Pauri, Uttar Pradesh, in central Himalaya, India, between 29°20′ and 30°15′N latitude and 78°10′ to 79°10′E longitude (TABLE 1). These sites repre-

TABLE 1. Characteristics of phenological events at three *Quercus leucotrichophora* forest study sites.

Site	Altitude m	Aspect	Community structure	Basal area of forest stand (m^2/ha)	Budbreak timing	Average leaf area (mm^2)
Randigad Panchayati Forest (RPF)	1160	NW	*Quercus leucotrichophora, Myrica esculenta, Pinus roxburghii, Sapium insigni*	14.00	March Third week	454.0
Thapli Village Panchayati Forest (RPF)	1570	N, NW	*Quercus leucotrichophora, Rhododendron arboreum, Myrica esculenta, Pinus roxburghii*	47.75	April First week	263.9
Nagdev Reserve Forest Compartment-2 (NAR-2)	1800	N, NW	*Quercus leucotrichophora, Rhododendron arboreum, Myrica esculenta, Lyonia ovalifolia, Aesculus indica*	32.15	April First week	247.3

sent three forest stands: Randigad Panchayati Forest (RPF), a banj oak forest at 1160 m; Thapli Village Panchayati Forest (TVPF), a banj-oak forest at 1570 m; and Nagdev Forest Range Compartment-2 (NAR-2), a mixed banj oak forest at 1800 m. Moisture availability is lower for RPF and increases through TVPF to NAR-2. Climatic data available from the Pauri station during a period of several decades revealed that the maximum rainfall occurs in rainy season (72%). Mean maximum temperature ranges between 9°C (January) and 24°C (May); the mean minimum temperature ranges between 2°C (January) and 16°C (July). The year is divisible into three main seasons: winter (October–February), summer (March–June), and rainy (July–September).

At each forest site, three healthy, medium size *Quercus leucotrichophora* trees were selected with more or less similar height (9–11 m) and circumference at breast height (85–90 cm). The trees, which grew naturally in open periphery with north-facing slopes, were surrounded by protective wire fencing. The entire canopy of each tree was arbitrarily divided into three positions: upper canopy (UC), middle canopy (MC), and lower canopy (LC).

During winter (second week of January) and well before the sprouting of buds, 540 healthy first-order lateral shoots were tagged with identification marks for periodical growth observations. The marks were made just below the neck of compact, healthy terminal vegetative buds, and the marked shoots included 20 shoots each from UC, MC, and LC positions of each tree at the three forest sites. The diameter at the base of the shoots was recorded with a digimatic caliper (Mitutoyo, Japan), and the length of shoots was taken using a tape. Buds harvested from other shoots were occasionally dissected under a field dissecting microscope to observe the bud primordia and other developmental stages, including bud gall infestation. The bud-break period was defined as the interval when the young leaves start protruding out of the bud scales in more than 25% of the shoots.

For statistical analysis, the author used measurements of shoot increments taken at the end of the growth period (first week of October) during both years of study. Two sets of shoot-increment data were taken: Shoots from all trees at each site were measured separately; and then shoots from all sites for each canopy layer (UC, MC, LC) were pooled to compare the outcome of total extension growth in relation to both site and canopy position. The author tallied parent shoot growth as last-year shoots (LYS) and new production as current-year shoots (CYS). For all tagged shoots, he computed last-year shoot length (LYSL), last-year shoot basal diameter (LYSD), current-year shoot length (CYSL) and current-year shoot basal diameter (CYSD). Also recorded were the number of leaves produced on last-year shoots (LYLS) and on current-year shoots (CYLS). Average leaf area was based on 100 mature leaves pooled from three current-year canopy layers in study trees at each site. An area meter (Delta Area Meter, RF-232C Interface, UK) was used for these measurements. The basal area of the banj oak stands was calculated in a separate study of tree population structure, by measuring circumference at breast height.

A separate 2-way ANOVA was carried out for each character for the three canopy layers in each of the three forest sites to test the significance of canopy position and forest site effect. Correlation analyses were made to establish the dependency of two variables in all three forest sites, and regression equations were obtained.

TABLE 2. Growth measurements for last-year and current-year shoots of mature *Quercus leucotrichophora* trees growing at three forest study sites, with mean values (bold type = areas of significance) and levels of significance.

Character	Mean values (bold = areas of significance)						Significance
LYSL (mm)	**RPF**	**171.56**	**TVPF**	**156.3**	NAR-2	106.7	***
	LC	158.8	MC	140.8	UC	134.96	N.S.
CYSL (mm)	**NAR-2**	**231.8**	**TVPF**	**203.6**	RPF	161.8	***
	LC	238.8	**UC**	**183.74**	**MC**	**174.7**	***
LYSD (mm)	TVPF	5.828	NAR-2	5.778	RPF	5.306	N.S.
	LC	**5.889**	**UC**	**5.824**	MC	5.198	*
CYSD (mm)	RPF	4.013	**TVPF**	**3.529**	**NAR-2**	**3.433**	***
	LC	**3.885**	**UC**	**3.746**	MC	3.343	***
LYLS (no.)	NAR-2	9.481	**TVPF**	**7.556**	**RPF**	**7.148**	***
	LC	8.185	MC	8.111	UC	7.885	N.S.
CYLS (no.)	NAR-2	11.259	**TVPF**	**9.519**	**RPF**	**8.778**	***
	LC	10.778	**UC**	**9.815**	**MC**	**8.963**	**

Note: RPF, TVPF, and NAR-2 are study sites spelled out in Table 1; * = significant at 5% level; ** = significant at 1% level; *** = significant at 0.1% level; N.S. = not significant; LYSL = last-year shoot length; CYSL = current-year shoot length; LYSD = last-year shoot diameter; CYSD = current-year shoot diameter; LYLS = last-year leaves; CYLS = current-year leaves; LC = lower canopy; MC = middle canopy; UC = upper canopy.

Frequency distribution for various classes of shoot length and diameter and number of leaves per shoot for both years at each forest site were analysed and plotted as histograms.

RESULTS

The basal area of forest stands at the three study sites was calculated as 14, 47.75, and 32.15 m^2/ha, respectively. The smallest average leaf area of *Quercus leucotrichophora* (247.3 mm^2) was found at the highest elevation (NAR-2); and the largest average leaf area (454 mm^2) was found at the lowest elevation (RPF); see TABLE 1. Difference in growth events was 7–15 days between lower and higher altitudes. Budbreak occurred in the third week of March at RPF and in the first week of April at TVPF and NAR-2. The maximum shoot increment was observed between March and August at all three sites.

The author tabulated extension growth (measured as shoot length), diameter, and number of leaves produced on last-year and current-year shoots at the three sites (TABLES 2, 3). Data indicated various levels of significance among different sets of parameters (TABLE 2). Last-year shoot length (LYSL) followed a decreasing order from RPF (171.56 mm) to NAR-2 (106.7 mm), with the latter differing significantly from the other two sites. The mean value of last-year shoots was greatest for the lower canopy (LC) and least for the middle (MC) and upper canopy (UC), although the differences were not significant. For current-year shoot length (CYSL), RPF with a 161.8 mm shoot differed significantly

TABLE 3. Regression equations for possible correlation of different characters in three *Quercus leucotrichophora* forests.

Forest site	Variable X	Variable Y	Regression equation	Correlation coefficient	Coefficient of determination
RPF	LYSD	CYSL	$Y = -90.5338 + 47.5213\ X$	0.7111	0.51
RPF	LYSD	CYSD	$Y = 1.0961 + 0.5363\ X$	0.7497	0.56
RPF	LYSL	LYLS	$Y = 4.8947 + 0.02028\ X$	0.7478	0.56
RPF	CYSD	CYSL	$Y = -127.1953 + 73.6631\ X$	0.7886	0.62
RPF	CYLS	CYSL	$Y = 119.3715 + 32.0668\ X$	0.8848	0.78
RPF	CYLS	CYSD	$Y = 1.4579 + 0.28595\ X$	0.7370	0.54
TVPF	CYSD	CYLS	$Y = 8.1215 + 4.9755\ X$	0.7731	0.60
NAR-2	LYSD	CYSD	$Y = 1.5398 + 0.32856\ X$	0.7299	0.53

Note: RPF, TVPF, and NAR-2 are forest study sites spelled out in Table 1; LYSL = last-year shoot length (mm); CYSL = current-year shoot length (mm); LYSD = last-year shoot diameter (mm); CYSD = current-year shoot diameter (mm); LYLS = last-year leaves (no.); CYLS = current-year leaves (no.).

from the other two sites which had similar CYSL (TABLE 1). Among canopy layers, current-year shoot length increased compared to last-year measurements. The lower canopy (LC) had a greater increase in current-year shoot length than did upper (UC) and middle canopy (MC), which had similar measurements. Current-year shoot diameter showed a decrease from last-year shoot diameter, which was similar at the three forest sites; however, current-year shoot diameter at the RPF (4.013 mm) did differ significantly from the other two sites. Among canopy layers, MC shoot diameter differed significantly from LC and UC positions, which had similar shoot diameters for both years (TABLE 2).

The number of leaves per shoot increased from parent (LYLS) to offspring (CYLS) in all cases (TABLE 2). Leaves survived the entire growth period. The smallest number of last-year and current-year shoot leaves were recorded at RPF (LYLS 7.148 and CYLS 8.778); and the largest number of shoot leaves occurred at NAR-2 (LYLS 9.481 and CYLS 11.259), as shown in TABLE 2. Shoots from NAR-2 differed significantly from the other two forests by number of leaves. Among canopy layers, the number of leaves on current-year shoots in the LC differed significantly from UC and MC at all three sites; however differences among canopy layers in number of leaves on last-year shoots were not significant.

Possible relations among different parameters and relevant regression equations are presented in TABLE 3. Except for one combination at each site, few significant correlations were obtained for TVPF or NAR- 2; but possible combinations were achieved for RPF. Relationships between CYSD and CYSL and between CYLS and CYSL are the most effective parameters chosen for RPF.

FIGURES 1 and 2 show the frequency distribution pattern of size classes for shoot length, shoot diameter, and number of leaves produced during the study's current year and last year at the three forest sites. Small to medium last-year shoots had low frequency distribution for all three sites (FIGURE 1). TVPF and NAR-2 had a greater number of medium-size shoots; and RPF had a greater number of smaller shoots. Among current-year shoots, the longest (particularly those 140–300 mm) had high frequency distribution for all sites. The higher frequency of current-year long shoots occurred for NAR-2 more than for the other two sites.

Last-year shoots generally represent a larger diameter class with a 40% frequency (FIGURE 2). Last-year shoots with 6–10 leaves and current-year shoots with 8–12 leaves recorded a higher frequency for all three sites. RPF current-year shoots are represented in each frequency class for number of leaves, with the largest number of shoots (39%) in the 8–10 leaf frequency class (FIGURE 2).

DISCUSSION

Quercus leucotrichophora, although similar to other late successional woody taxa (Ramakrishnan et al. 1982), does not have the short-term growth flushes (indeterminate pattern) of *Q. palustris* (Borchert 1975). *Quercus leucotrichophora* has a determinate pattern of shoot growth, with growth usually limited to winter bud contents (Badola 1991, Badola et al. 1992). Shoots fully pre-formed in winter buds use large amounts of reserve carbohydrates during early elongation (Kozlowski & Winget 1964, Badola & Paliwal 1986). Shoot formation involves differentiation in the bud during the first year and expansion of the pre-formed contents into a shoot in the second year (Sacher 1954, Kozlowski 1963, Badola & Paliwal 1987, Badola 1991, 1994). Elevation may contribute to generate intraspecific differences in phenotypic plasticity (Montenegro et al. 1997), demonstrated in *Q. leucotrichophora* by the difference of 15 days in bud-break time between lower and higher altitudes. Delayed bud-break at higher elevation, however, may be related to smaller leaf area (Rusch 1993).

The flushing or rapid shoot growth period constitutes a critical phase, during which the trees make heavy use of resources taken from the environment. Such resources will later be allocated for other activities such as secondary growth (Montenegro et al. 1997). Thus knowledge of the time of bud break in spring and subsequent growth flushing will be useful for the conservation and management planning of banj oak forests. Forest treatments during the bud flushing period should be limited to lopping twigs. This period may be related to the unidentified "cynapid" insect infestation that has caused bud-gall formation in *Quercus leucotrichophora* shoots. The infestation could become an epidemic for entire forest stands (Badola 1994).

The author obtained variations in extension growth for all three study sites. Variability in shoot size within plant parts may reflect key differences in internal resource availability or resource-capturing ability. Such variability may be more relevant than age as a classification variable (McGraw 1989). The small current-year shoots at RPF may reflect higher deployment of photosynthate in the development of large leaves. McGraw (1989) observed in *Rhododendron maximum* that large last-year shoots

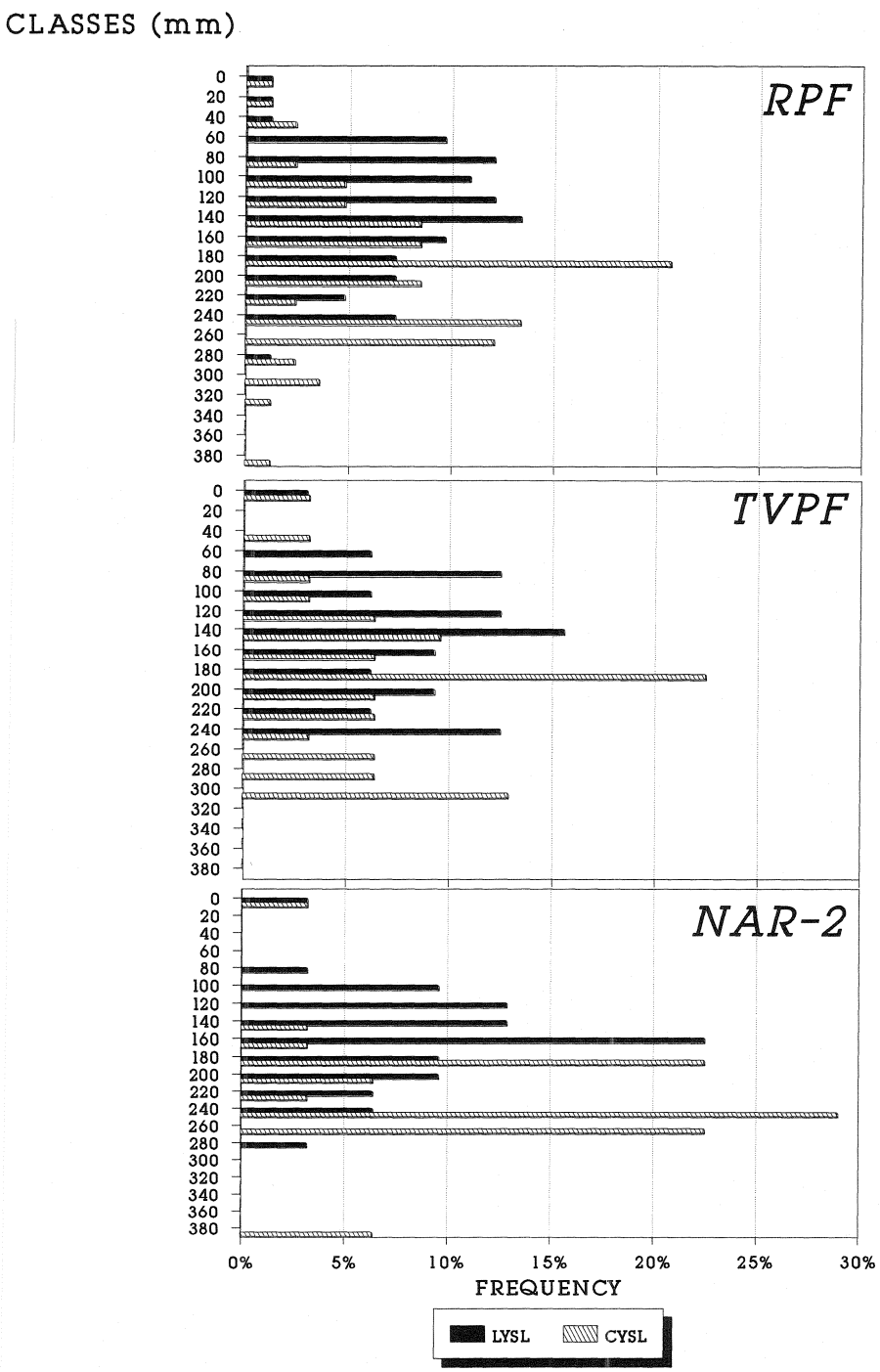

FIGURE 1. Frequency distribution (%) for different size (length) classes of last-year and current-year shoots of *Quercus leucotrichophora* trees growing in three forest sites: Randigad Panchayati Forest (RPF), Thapli Village Panchayati Forest (TVPF), and Nagdev Range Compartment 2 (NAR-2). Note: LYSL = last-year shoot length and CYSL = current-year shoot length.

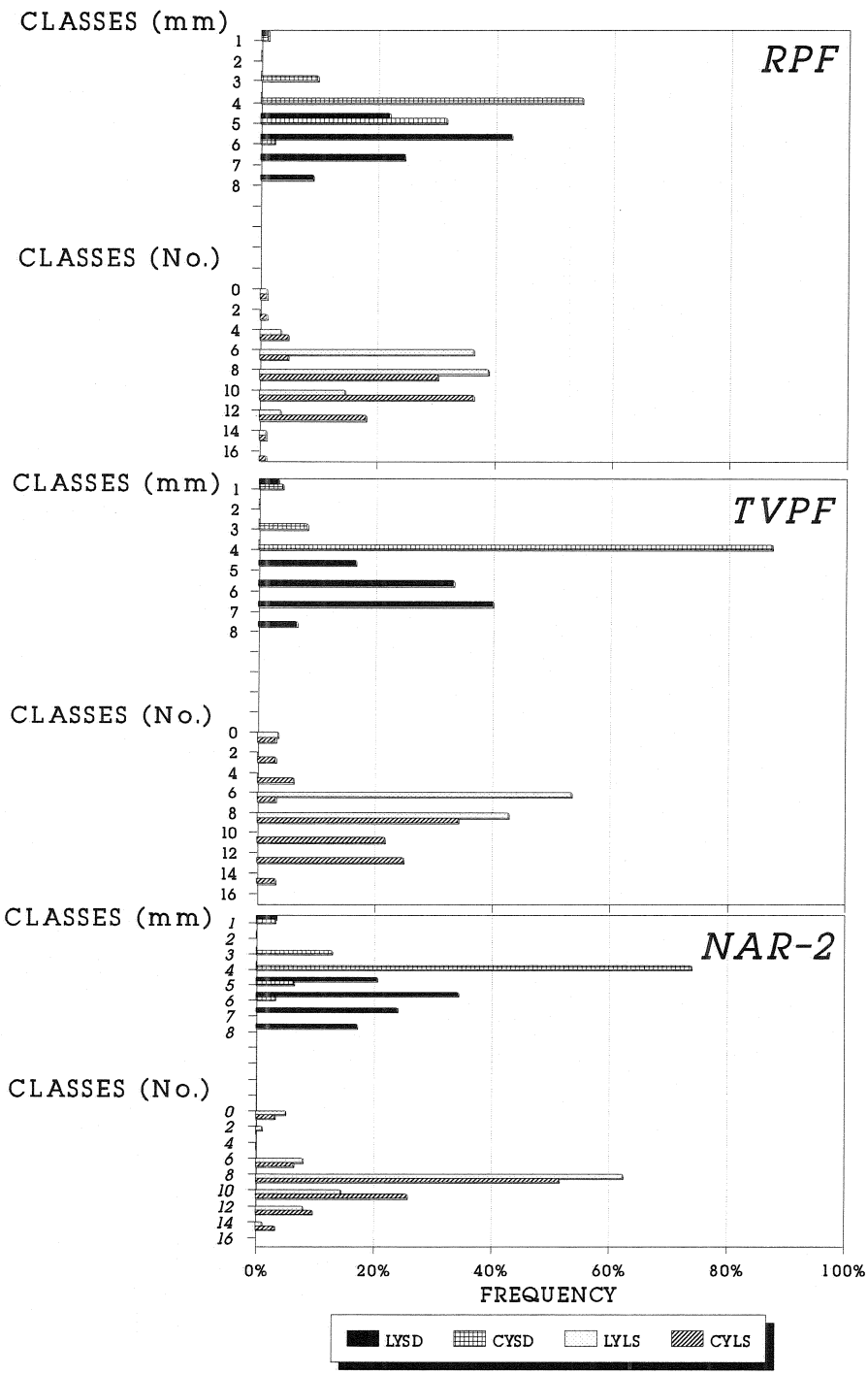

FIGURE 2. Frequency distribution (%) for different classes of last-year and current-year shoots of *Quercus leucotrichophora* trees for diameter and number of leaves (per shoot), growing at study sites in RPF, TVPF, and NAR-2. Note: LYSD = last-year shoot diameter, CYSD = current-year shoot diameter, LYLS = last-year leaves, and CYLS = current-year leaves.

remained large in current-year data. In *Quercus leucotrichophora,* however, the size of current-year shoots exceeded last-year data. A closer relationship exists between the amount of shoot growth and the weather in the year of bud formation than in the year of shoot expansion (Kozlowski 1964, Kozlowski & Keller 1966). Trends in shoot extension in *Q. leucotrichophora* with respect to weather at various forest sites need to be explored.

In shoot populations, parental care (Fetcher & Shaver 1983) takes the form of translocation of internal resources from the parent shoot to the daughter shoot (McGraw 1989). In *Quercus leucotrichophora,* the increasing number of leaves from parent shoots to offspring shoots may be related to the similar nature of parental care. Such pattern of translocation may improve the chances of survival of vegetative offspring (Ashmun et al. 1982). *Q. leucotrichophora* leaves remain on the shoots during the entire annual growth period. In evergreen species, the leaves of parent shoots often remain alive for long periods and may serve as the primary source of carbon and nutrient resources (McGraw 1989).

With a determinate pattern of growth, the number of leaves on current-year shoots indicate the number of leaf primordia or stem units preformed in the last winter bud. The number of leaves may be an expression of the amount of free growth, as with needle formation in *Picea abies* (Ununger & Kang 1988). An established relationship exists between the number of stem units (an indicator of bud size) and expected shoot length in the next season (Lanner 1971, Kozlowski 1973). Using the number of leaf primordia in an unopened bud of *Quercus leucotrichophora* as an indicator of future extension growth, however, remains hypothetical, since the data from TVPF and NAR-2 are inconclusive.

A population of current shoots on a tree or a single branch can be described by shoot-length frequency distribution (Wilson 1990). In *Quercus leucotrichophora,* large numbers of current-year long shoots may be related to a competitive attribute, involving production and deployment of large amounts of photosynthates (Grime 1979). In NAR-2, such deployment of photosynthate may relate to the formation of longer shoots and greater numbers of leaves than to producing large leaves, as at RPF.

In *Quercus leucotrichophora,* where shoot growth is predetermined during the previous growth period, temperature as well as day length could affect the number of pre-formed nodes and leaves within the resting bud (Longman 1990). Current-year shoots generally have a smaller diameter but greater number of leaves compared to last-year shoots. The greater number of leaves on current-year shoots can be linked to higher productivity resulting from a competitive attribute (Grime 1979). The entire banj oak analysis supports the claim of Watson and Casper (1984) that most plants do not behave as completely integrated entities but more as populations of relatively independent physiological units. Although the banj oak analysis provides baseline data on the shoot-growth behavior of these trees, more experiments are required to achieve a better understanding.

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